1st Interdisciplinary Navigation Symposium

26-30 June 2016
HOTEL DE L'EUROPE
Kaiser Franz Joseph-Straße 14
5640 Bad Gastein, Austria

REGISTRATION
Sunday 26th 16.00-18.00
Monday 27th 8.00-8.45
Hotel De l'Europe

BRING YOUR OWN
COMPUTER if you are presenting as an Invited Speaker.

WELCOME RECEPTION
Sunday 26th 18.00-20.00
• Drinks and Snacks •
Waterfall Power Plant

CONFERENCE DINNER
Thursday 30th 19.30
• 5-course menu •
Hotel Miramonte

Organizers: Dave Dickman, Kate Jeffery, Mayank Mehta, Laure Rondi-Reig, Jeffrey Taube, Thomas Wolbers
Taxis

There are two taxi companies for your rides around Bad Gastein:

<table>
<thead>
<tr>
<th>Taxi Schett OG</th>
<th>Taxi Giorgi</th>
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<tbody>
<tr>
<td>Karl-Heinrich-Waggerl-Str. 45</td>
<td>Kaiser-Franz-Josef-Str. 5</td>
</tr>
<tr>
<td>5640 Bad Gastein</td>
<td>5640 Bad Gastein</td>
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<tr>
<td>ph. +43-6434-2713</td>
<td>ph. +43-6434-30 143</td>
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<td><a href="mailto:info@badgasteintaxi.at">info@badgasteintaxi.at</a></td>
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Internet acces

There is free internet access at Hotel de l’Europe (Venue) for all attendees during the conference. You will get login details upon registration.

Poster Presentation

For those presenting a Poster during the conference please put up your poster until **15:00 on Monday 27th**. Look for your name on the poster boards and place your poster there.

Pins are provided.

Poster Presenters are asked to be present at their posters during both slots: **Monday, 27th 18.30-19.30** and **Tuesday, 28th 17.30-18.30** (as can be seen in the program)

*Remind to take down your poster on either Wednesday afternoon/evening or Thursday morning!*

Outings

On Wednesday 29th between 14:30 - 17:30 we have planned some time for outings such as guided hikes, bike tours, historical walk, cable car ride up the mountains, Yoga, ...

**Enrollment:** Upon registration but no later than **Monday, 27th 14:00**

**Costs:** € 5,- to € 34,- *(payable in cash to the guide just before the tour starts)*

**Meeting point:** Entrance of Hotel De l’Europe (Venue) for all tours except Yoga (Hotel Miramonte).

**Bring:** Hiking boots, Sports wear if you are interested in a physical activity.

Welcome Reception

To meet your colleagues before the conference starts you are invited to our Welcome Reception with drinks and snacks (included in registration fee).

When?  Sunday, 26th  18.00 - 20.00
Where?  Waterfall Power Plant, Wasserfallstraße 7, 5640 Bad Gastein
How?  You can walk in 10 min via Kaiser-Franz-Josef-Str., Straubingerplatz and Bismarckstr. down to the Waterfall Power Plant.

Conference Dinner

The conference dinner will be held on the last evening after the end of the conference (included in registration fee).

When?  Thursday, 30th  19:30
Where?  Hotel Miramonte, Reitlpromenade 3, 5640 Bad Gastein
How?  You can walk in 15 min via Kaiser-Franz-Josef-Str., Straubingerplatz, Bismarckstr. and the walkway to Hotel Miramonte.
Restaurants

As there is low season in Bad Gastein at the end of June some restaurants are still closed.
To avoid disappointment we have listed some restaurants that are open (please note opening
hours and reservation details):

Lutter & Wegener (Fine Austrian and International Cuisine)
Kaiser-Franz-Josef-Straße 16, 5640 Bad Gastein
www.villasolitude.com, info@villasolitude.com, ph. +43 6434 5101
mon, tues, wed from 6.00 pm - 9.30 pm - Reservation recommended!

Das Regina (International Culinary Creativity)
Karl Heinrich Waggerl Straße 5, 5640 Bad Gastein
www.dasregina.com, welcome@dasregina.com, ph. +43 6434 2161 0
daily from 7.00 am - 9.00 pm - Reservation recommended! (for groups over 10 people 1 day in advance)
Bar: - 0.00

Ginger & Gin at Hotel de l’Europe (Asian Inspired Creativity)
Kaiser Franz Josef-Straße 14, 5640 Bad Gastein
www.gingerandgin.at, goodtimes@gingerandgin.at, ph. +43 676 750 2626
daily from 6.00 pm - 10.00 pm - Reservation recommended! Bar: - 2.00 am

Wirtshaus Jägerhäusl (Austrian Kitchen + Pizza)
Kaiser-Franz-Josef-Straße 9, 5640 Bad Gastein
www.gastrogastein.at, ph. +43 6434 20254 or +43 0664 5808746
daily from 12.00 am - 10.00 pm - Reservation required for groups over 8 persons!

Steak & mehr (Steakhouse)
K. H. Waggerl-Straße 32, 5640 Bad Gastein
www.steakmehr.at, steak@steak-mehr.at, ph. +43 6434 30131
tues, wed, thurs from 10.00 am - 10.00 pm - Reservation recommended!

Haus Hirt (International Culinary Creativity)
Kaiserhofstrasse 16, 5640 Bad Gastein
www.haus-hirt.com, info@haus-hirt.com, ph. +43 6434 2797 47
daily from 6.30 pm - 9.00 pm - Reservation required 24 hours in advance!

Miramonte (International Culinary Creativity)
Reitlpromenade 3, 5640 Bad Gastein
www.hotelmiramonte.com, info@hotelmiramonte.com, ph. +43 6434 25770
daily from 6.30 pm - 9.00 pm Bar: open end - Reservation required 24 hours in advance!

Bellevue Alm (Austrian Kitchen)
Bellevue Alm Weg 6, 5640 Bad Gastein
www.bellevuealm.at, info@bellevuealm.at, ph. +43 6434 3881
daily from 10.30 am - 12.00 pm - Reservation required for big groups!

Orania Stüberl (Austrian Cuisine)
Bahnhofplatz 2b, 5640 Bad Gastein, ph. +43 6434 6264
mon, tues, thurs from 11.00 am - 9.00 pm - Reservation required for big groups!

Ritz (Austrian and International Cuisine)
Grillparzerstrasse 1, 5640 Bad Gastein
hotel@salzburgerhof.com, ph. +43 6434 2037 540
mon, tues from 6.00 pm - 9.00 pm - Reservation recommended!

Angelo’s (Original Italian Food)
K.H. Waggerl-Straße 16, 5640 Bad Gastein
hotel@salzburgerhof.com, ph. +43 6434 20760 720
mon, tues, thurs from 6.00 pm - 10.00 pm - Reservation recommended!

Please note that we do not guarantee for the quality of the restaurants.
## Program iNAV 2016

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<td>Nolan, Matt</td>
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<td>Angelaki, Dora</td>
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<td>Glasauer, Stefan</td>
<td>Probabilistic estimation in simple navigation tasks</td>
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<td>Barry, Caswell</td>
<td>Is there a role for grid cells in navigation?</td>
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<td>Herz, Andreas</td>
<td>Decoding the population activity of grid cells for spatial localization and goal-directed navigation</td>
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<td>Serdič, Shiša</td>
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<td>Dudchenko, Paul</td>
<td>Place cell repetition, spatial learning, and the head direction cell system</td>
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<td>Nitz, Douglas</td>
<td>Encoding of spatial axes and analogies in the dorsal subiculum</td>
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<td>Laurens, Jean</td>
<td>Three-dimensional tuning of head direction cells in rodents</td>
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<td>Dickman, David</td>
<td>Head direction cells in the macaque brain</td>
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<td>15:30 - 16:00</td>
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<td>16:00 - 17:30</td>
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<tr>
<td>Yoder, Ryan</td>
<td>Otolith signals contribute to heading direction but not place recognition: evidence from further tests on the Barnes maze</td>
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<tr>
<td>Cullen, Kathleen</td>
<td>Vestibular processing during natural self motion: Implications for perception and action</td>
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<td>Smith, Paul</td>
<td>Vestibular inputs to the hippocampus</td>
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<td>Rondi-Reig, Laure</td>
<td>Navigation under cerebellar-hippocampal coupling</td>
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<td>17:30 - 18:30</td>
<td>Data Blitz Session 1</td>
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<tr>
<td>Sarel, Ayelel</td>
<td>Vectorial representation of spatial goals in the hippocampus of bats</td>
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<td>Bush, Daniel</td>
<td>Grid cell phase coding in the absence of rhythmicity</td>
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<tr>
<td>Dumont, Julie</td>
<td>Neural correlates within nucleus prepositus and paragigantoce llaris during active and passive movement</td>
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<tr>
<td>Geva-Sagiv, Maya</td>
<td>Orthogonal hippocampal maps for different sensory modalities in flying bats</td>
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<tr>
<td>Li, Shu-chun</td>
<td>Dopamine modulation of the hippocampal-striatal circuitry: implications for the aging of spatial learning and memory</td>
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<td>Quirk, Clare</td>
<td>Optogenetic stimulation of parvalbumin neurons in the medial septum paces theta frequency and disrupts spatial memory</td>
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<tr>
<td>Riemer, Martin</td>
<td>Cognitive maps are influenced by body location</td>
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<td>Navarro Schroeder, Tobias</td>
<td>Trigonometry predicts entorhinal processing of reference points</td>
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<tr>
<td>Winter, Shawn</td>
<td>Grid cell representation across a multi-level maze</td>
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<td>Zutshi, Ipshita</td>
<td>Functional characterization of recurrent networks within superficial layers of the medial entorhinal cortex</td>
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<td>Session 5</td>
<td>Girard, Benoît: Computational models of navigation strategies and their coordination: rodents &amp; robots  &lt;br&gt; Mizumori, Shéri: Hippocampal neural activity reflects the economy of choices during navigation  &lt;br&gt; Wiener, Sidney: Activity in hippocampal afferent striatal zones  &lt;br&gt; van der Meer, Matthias: Model-based influences on the content of hippocampal sequences</td>
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<tr>
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<td>11:00 - 12:30</td>
<td>Session 6</td>
<td>Cacucci, Francesca: Developing neural maps of space, in the hippocampus and beyond  &lt;br&gt; Epstein, Russell: Geometric reorientation mechanisms in the rodent and human brains  &lt;br&gt; Mou, Weimin: Superior cognitive mapping through single-landmark-related learning than through boundary-related  &lt;br&gt; Knierim, Jim: Local cue influences on place cells: Object vectors and floor texture boundaries</td>
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<td>Session 7</td>
<td>Warren, William: From cognitive maps to cognitive graphs  &lt;br&gt; Milford, Michael: From rats to robot navigation and back again  &lt;br&gt; Newcombe, Nora: Do people form cognitive maps? An individual differences approach  &lt;br&gt; Wang, Frances: How can a cognitive map evolve from the path integration system</td>
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<tr>
<td>15:30 - 15:45</td>
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<tr>
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<td>Topic Discussion 1: What general principles about navigation can we extract across different species?</td>
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<td>Data Blitz Session 2</td>
<td>Bellmund, Jacob: Grid-cell representations in mental simulation  &lt;br&gt; Chen, Xiaoli: Hippocampal volume predicts spatial navigation performance with landmark cues in humans  &lt;br&gt; Chan, Dennis: Spatial memory testing in pre-dementia Alzheimer's disease  &lt;br&gt; Kuruvilla, Maneesh: The role of entorhinal cortex in local and global spatial memory  &lt;br&gt; Lazaridou, Athina: Navigating multi-level complex museum environments  &lt;br&gt; Maldenbaum, Shachar: Comparatively exploring the neural basis for visual and auditory interactive virtual navigation in humans who are congenitally blind, briefly visually deprived and sighted  &lt;br&gt; Sutton, Jennifer: Cognitive maps across adolescence  &lt;br&gt; Takemiya, Makoto: Implication of adaptive wayfinding aids  &lt;br&gt; Wood, R: The effect of hippocampal and medial entorhinal cortical lesions on the learning of a novel test of allocentric spatial memory  &lt;br&gt; Zhang, Lei: When boundary-related learning is not incidental: Perceived stability modulates cue-selection process in goal localization  &lt;br&gt; Zhou, Ruojing: Position and heading estimations during driving in a large scale environment</td>
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<tr>
<td>17:30 - 18:30</td>
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### Wednesday 29 June

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<th>Time</th>
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<tbody>
<tr>
<td>9:00 - 10:30</td>
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<td>Wolbers, Thomas: Mechanisms of location coding in the human brain  &lt;br&gt; McNamara, Timothy: Comparative investigations of human navigation  &lt;br&gt; Barnes, Carol: Recent progress in recording from completely unrestrained primates  &lt;br&gt; Mehta, Wayank: Bridging Rodent Human divide: Place cells during virtual navigation</td>
</tr>
<tr>
<td>10:30 - 10:45</td>
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<td>Session 9</td>
<td>Burgess, Neil: Neural mechanisms of navigation and imagery  &lt;br&gt; Avraamides, Marlos: Spatial representations for immediate and remote environments; their role in navigation  &lt;br&gt; Galati, Gaspare: Coding of spatial locations during scene recognition and imagery  &lt;br&gt; Meilinger, Tobias: Spatial integration within large-scale spaces</td>
</tr>
<tr>
<td>13:00 - 14:00</td>
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<tr>
<td>14:30 - 17:30</td>
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iNAV 26 - 30 June 2016  
Errors and omissions excepted.
## Session 10

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<th>Time</th>
<th>Session 10</th>
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</table>
| 9:00 - 10:30  | Taube, Jeffrey: The head direction cell attractor network: if there is one, where is it located?  
|               | Jayaraman, Vivek: The neural dynamics of fly navigation                      |
|               | Jeffery, Kate: Multiple head direction cell reference frames in retrosplenic cortex  
|               | Zhang, Kechen: Multistability of attractor spatial maps                      |

## Session 11

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<tbody>
<tr>
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<td>Coffee</td>
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</table>
| 11:00 - 12:30 | Battaglia, Francesco: Neural oscillations and navigational strategies       
|               | Colgin, Laura: Spatial memory operations during slow and fast gamma rhythms in the hippocampus  
|               | Buffalo, Elizabeth: Neural activity in the macaque hippocampus during virtual navigation  
|               | Jacobs, Joshua: Direct brain recordings reveal how the human brain represents space |

## Lunch

**12:30 - 14:00**

## Session 12

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<th>Time</th>
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| 14:00 - 15:45 | Giudice, Nicholas: Multimodal spatial technologies for sensory substitution and compensatory augmentation  
|               | Wiener, Jan: The effects of typical and atypical ageing on orientation and navigation behaviour  
|               | Hegarty, Mary: Towards an understanding of Individual differences in human navigation  
|               | Iaria, Giuseppe: Developmental topographical disorientation: Some insights  
|               | Ishikawa, Toru: Maps in the head and tools in the hand: Spatial awareness in a spatially enabled society  |

## Coffee

**15:45 - 16:00**

## Session 13

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| 16:00 - 17:30 | Ulanovsky, Nachum: Neural basis of 3D goal-directed navigation in bats       
|               | Bingman, Vern: Homing pigeons on autopilot: Ethological revelations into hippocampal-dependent perceptions of  
|               | Golani, Ilan: Two presumably homologous navigation systems in arthropods and vertebrates  
|               | Cheng, Ken: Views, active vision, and navigating brains: An insect perspective |

## Topic Discussion 3: Neural and Behavioural Processes in Navigation / Individual Differences

**17:30 - 18:15**

## Wrap-up & Final Thoughts

**18:15 - 18:30**

## Conference Dinner at Hotel Miramonte

**19:30**
 Registered Participants iNAV 2016

James Ainge | University of St Andrews
Andrew Alexander | University of California San Diego
Kevin Allen | Heidelberg University / DKFZ
Dora Angelaki | Baylor College of Medicine
Dian Anggraini | Ludwig-Maximilians-University Munich
Marios Avraamides | University of Cyprus Nicosia
Carol Barnes | University of Arizona
Caswell Barry | University College London
Joshua Bassett | University College London
Francesco Battaglia | Radboud University Nijmegen
Marcia Bécu | Institut de la Vision, Paris
Jacob Belimund | Radboud University Nijmegen
Verner Bingman | Bowling Green State University Ohio
Emily M. Blackwood | University of Maine
Michael Bond | Journalist UK
Jacob Bruce | Queensland University of Technology
Elizabeh Buffalo | University of Washington
Neil Burgess | University College London
Ford Burtes | University of Calgary
Daniel Bush | University College London
Francesca Cacucci | University College London
Fabrizio Capitano | LNC Aix-Marseille Université
Dennis Chan | University of Cambridge
Guilien Chen | University College London
Xiaoli Chen | DZNE Magdeburg
Ken Cheng | Macquarie University
Han Yin Cheng | University College London
Laura Colgin | University of Texas at Austin
Joszef Csicsvari | IST Austria Klosterneuburg
Kathleen Cullen | McGill University
Dori Derdikman | Technion Haifa Israel
David Dickman | Baylor College of Medicine
Paul Dudchenko | University of Stirling
Julie Dumont | Dartmouth College Hanover
Eleonore Duvelle | University College London
Vegard Edvardsen | Norwegian University of Science and Technology Trondheim
Tamra Eliaj | Weizmann Institute of Science
Russell Epstein | University of Pennsylvania
Virginia Flanagin | German Center for Vertigo and Balance Disorders, LMU Munich
Gaspare Galati | Sapienza University
Maya Geva-Sagiv | Weizmann Institute of Science Israel
Eugenio Gianni | Uniti Rovereto
Benoit Girard | CNRS - UPM C Paris
Nicholas Giudice | University of Maine
Stefan Glasauer | Ludwig-Maximilians-Universität München
Ilan Golani | Tel Aviv University
Roddy Grieves | University College London
Ramona Grzeschik | Bournemouth University
Gengen He | University of Nottingham China
Mary Hegarty | University of California Santa Barbara
Andreas Herz | Bernstein Center and LMU Munich
David Howett | University of Cambridge
Giuseppe Iaria | University of Calgary
Toru Ishikawa | University of Tokyo
Pierre-Yves Jacob | University College London
Joshua Jacobs | Columbia University New York
Vivek Jayaraman | Janelia Research Campus, Howard Hughes Medical Institute
Kate Jeffery | University College London
Joshua Julian | University of Pennsylvania
Ingmar Kanitscheider | University of Texas at Austin
Amitay Katz | Tel Aviv University
Alexander Keinath | University of Pennsylvania
James Kneelam | Johns Hopkins University
Olga Kornienko | Heidelberg University / DKFZ
Maneesh Kuruvilla | University of St Andrews
Rune Latuske | University of Oslo
Patrick Latuske | Heidelberg University / DKFZ
Jean Laurens | Baylor College of Medicine
Athina Lazaridou | The Bartlett School of Architecture, UCL
1. Spatial geometry orients hippocampal spatial representations in disoriented mice

Alex T. Keinath - University of Pennsylvania, Joshua B. Julian - University of Pennsylvania, Russell A. Epstein - University of Pennsylvania, Isabel A. Muzzio - University of Texas: San Antonio

The ability to regain one’s bearings when lost or disoriented is crucial to successfully navigating in a complex, unstable world. An extensive literature, extending back 25 years, indicates that many species, from ants to humans, primarily rely on spatial geometry, i.e. the shape of the navigable space, to reorient themselves after becoming disoriented. However, little is known about the neural mechanisms underlying this behavior. Here we tested the hypothesis that spatial geometry, rather than non-geometric features, controls the orientation of hippocampal spatial map in disoriented mice, and that the orientation of this map is intimately linked to reorientation behavior. First, we recorded hippocampal CA1 place cells of disoriented mice foraging in three environments, each with a unique geometry and polarizing visual cue. Each environment elicited a reliable hippocampal map, and as we predicted the orientation of this map was determined by the spatial geometry, not the polarizing visual cue. Second, we recorded from place cells in CA1 as disoriented mice completed a classical reorientation task in which they were trained to find a reward hidden in one of four cups placed in a rectangular environment containing a polarizing visual cue (Cheng, 1986). Once again, we found that the orientation of the hippocampal map was controlled by geometry; moreover, the orientation of the map predicted the corner in which the animal searched for the reward in on a trial-by-trial basis. These results illuminate the neural mechanisms underlying reorientation behavior by showing that the orientation of the hippocampal map is primarily controlled by spatial geometry and this map in turn predicts the spatial behavior of the animal.

2. Context recognition and heading retrieval have dissociable effects on hippocampal spatial representations

Joshua B. Julian [1], Alex T. Keinath [1], Russell A. Epstein [1], Isabel A. Muzzio [2]
1 - Department of Psychology, University of Pennsylvania, Philadelphia, PA
2 - Department of Biology, University of Texas: San Antonio, San Antonio, TX

A lost navigator must identify his current location and recover his facing direction in order to restore his bearings. We recently found behavioral evidence that these two processes—context recognition and heading retrieval—are mediated by dissociable cognitive systems in mice (Julian et al., 2015). In particular, we observed that although non-geometric visual features are used for context recognition, those same cues are ignored for heading retrieval, which is instead guided primarily by spatial geometry. Here we test the idea that these two processes have dissociable influences on hippocampal spatial representations. We recorded from hippocampal CA1 place cells of disoriented mice trained to locate rewards in two rectangular chambers that were geometrically identical but distinguishable based on non-geometric features along the walls. The features could be used to both identify the chambers (context recognition) and to disambiguate facing directions within the chambers (heading retrieval). We found that the orientation of the place field map within each chamber was determined by the spatial geometry. Across trials, two orientations of the place field map were observed, one being the 180° rotation of the other. However, we also observed rate remapping between the two chambers; place cells were active in the same location in the two chambers relative to the chamber geometry, but their firing rates reliably differed between the two chambers. Thus, the non-geometric features affected place cell firing rates, but did not affect the orientation of the map. The orientation of the place field map and the place cell firing rates predicted distinct aspects of the animals’ spatial behavior on a trial-by-trial basis. These results suggest that the hippocampus receives input from dissociable pathways for spatial geometry and visual features, and provide further support for the existence of separate systems for context recognition and heading retrieval.

3. Contribution of cerebellar PF-PC LTP to spatial map stability

Julie M. Lefort1,2,3, Frederic Jarlier1,2,3, Chris I. De Zeeuw4,5, Laure Rondi-Reig1,2,3,* and Christelle Rochefort1,2,3*
1 Sorbonne Universités, UPMC Univ Paris 06, UMR-S 8246, Neuroscience Paris Seine, Cerebellum Navigation and Memory (CeZaMe) team, F-75005, Paris, France 2 INSERM, UMR-S 1130, Neuroscience Paris Seine, Cerebellum Navigation and Memory (CeZaMe) team, F-75005, Paris, France 3 CNRS, UMR 8246, Neuroscience Paris Seine, Cerebellum Navigation and Memory (CeZaMe) team, F-75005, Paris, France 4 Department of Neuroscience, Erasmus MC, 3000 DR Rotterdam, The Netherlands 5 Netherlands Institute for Neuroscience, Royal Academy of Sciences (KNAW), Meibergdreef 47, 1105 BA Amsterdam, The Netherlands

* Equal contribution.
Several plasticity sites have been described in the cerebellar cortex, among which the Parallel Fiber-Purkinje Cell synapse, displaying both Long Term Depression (LTD) and Long Term Potentiation (LTP), has received most interest. We previously showed that a lack of PF-PC LTD altered self-motion processing and subsequent dependent hippocampal processes, i.e. maintaining a cognitive representation of space using self-motion information and using it for optimal goal-directed behavior. However, it remains unclear if these navigation processes specifically depend on cerebellar LTD per se or ensue from a general disruption of cerebellar circuitry. To test this we investigated the functional consequences of a deficit of LTP at PF-PC synapses using L7-PP2B mice model. Hippocampal place cell properties of L7-PP2B mice were characterized during free exploration of a circular arena. In contrast to mice lacking cerebellar LTD, place cell properties of L7-PP2B mice were not impaired when mice had to rely on self-motion cues. Surprisingly, L7-PP2B place cells displayed instability in the absence of any proximal cue manipulation in 20 % of the recording sessions, characterized by a coherent angular rotation of the whole set of recorded place cells. During these events, in which the spatial relationships between the object and the mouse spatial representation are changed, mice displayed an increased exploration of the object, suggesting that for the mouse the object was located at a new position. These data suggest that, in the absence of cerebellar LTP, hippocampal spatial representation cannot be reliably anchored to the prominent external cue. These results along with those from L7-PKCI mice, indicate that the cerebellum might be involved in multiple sensory processing required to navigate properly.

4. Feel the way: Does a vibrotactile compass help you learn a space?

Steven M. Weisberg, Center for Cognitive Neuroscience, University of Pennsylvania
Daniel Badgio, Center for Cognitive Neuroscience, University of Pennsylvania
Anjan Chatterjee, Center for Cognitive Neuroscience, University of Pennsylvania

Navigating in complex indoor spaces (e.g., libraries, hospitals, and airports) makes one effective strategy - maintaining bearings - very difficult because of the labyrinthine routes and lack of distal cues. Ordinarily, compasses provide bearings, but they draw attention and gaze away from the visual scene, and are not useful for blind navigators at all. With advancements in technology, however, bearings can be provided in a vibrotactile manner (through a ring of motors worn on the arm, which is programmed to vibrate in a constant cardinal direction). We hypothesized that providing bearing information boosts spatial navigation specifically for tasks requiring access to directional information. Alternatively, providing bearing information may promote general spatial navigation (e.g., through enhanced attention), in which case many tasks should benefit. We developed two routes through a large, complex hospital. In a counter-balanced within-subjects design, we taught participants one route with the vibrotactile compass, and one route without. Participants were tested by pointing to specific points: external landmarks outside the hospital, and internal landmarks, learned along the route; and pointing to match directions: cardinal directions (point East), and landmark directions (point the direction faced when viewing an internal landmark). Participants also had to reverse the route, draw a sketch map, and answer questions about strategies. In line with our hypothesis, we predicted that only pointing to match directions should show improvement. These tasks require the least computation to perform more accurately when a bearing is provided compared to the other spatial tasks. Preliminary results support our hypothesis - only pointing to match direction judgments were enhanced when participants wore the vibrotactile compass. We suggest that a vibrotactile device can actually enhance spatial representations, but does so in a specific way.

5. Towards bat hippocampal recordings in large-scale environments

Tamir Eliaav1, Liora Las1, Nachum Ulanovsky1
1. Department of Neurobiology, Weizmann Institute of Science, Rehovot 76100, Israel

For the last forty years, hippocampal research has typically focused on spatial representations in small laboratory environments. Nothing is known about hippocampal neural codes on large spatial scales – in environments spanning hundreds of meters or kilometers – the scales of natural navigation by rodents and other mammals. Here we aim for the first time to develop a unique recording setup, including a large-scale ethologically relevant environment, which will allow us to address this fundamental question. We are using the Egyptian fruit bat, because (i) bats are excellent navigators over large natural scales, and (ii) bats were shown to have rodent-like hippocampal spatial representations in small laboratory environments. So far, we took the following steps: First, we developed an on-board wireless neural-logging system, which allows recording single-units over unlimited distances. Second, we built a 200-m long tunnel where bats can fly freely. Third, to track the bat’s position we utilized an RF localization device that measures distances to an antenna-array – yielding a spatial accuracy of ~10-cm, much better than GPS. Preliminary experiments showed that bats fly volitionally back-and-forth along the tunnel – up to 100 laps per session (20-km total flight distance). We hypothesize two possibilities for hippocampal coding of large-scale environments: (i) enlargement of place-fields to dozens of meters, versus (ii) hundreds of small place-fields for each place-cell. Here we will present the first neural recordings that directly test these hypotheses.
6. **Retrosplenial cortex spatial firing patterns represent sub-spaces within broader routes**

Andrew S. Alexander and Douglas A. Nitz  
Department of Cognitive Science, University of California, San Diego

Recent work from our laboratory examined the potential role of retrosplenial cortex (RSC) in encoding conjunctions of spatial information of qualitatively different types. RSC neuron ensembles effectively encoded the left versus right turning behavior of rats traversing three-turn sequences along paths through an environment indicating a mapping of spatial information in one or more egocentric frames of reference. The same ensembles contained neurons whose positional rate vectors distinguished positions across the same paths, thereby providing spatial information in a route-based frame of reference above and beyond what could be accounted for by firing correlates to specific actions. Nevertheless, largely distinct route-position-encoding ensembles were observed when the path occupied different locations within the larger environment. Thus, RSC maps position within complex routes and the position of routes within an environment. The present work further examined the positional firing properties of RSC neurons as animals traversed the perimeter of a plus-shaped track at a fixed location in the environment. Full track traversals returned the animal to its starting location after executing a complex, yet recurring, turn sequence. The recurrent structure of the track yielded RSC spatial firing rate profiles that segmented the full route into repeating patterns representing sub-spaces within the full trajectory. These sub-space representations were most commonly found for quarter and half route segmentations, suggesting RSC may extract sub-space information at specific spatial scales. Interestingly, half route segmentations may reflect a novel form of spatial mapping found in RSC, by which single RSC neurons track the animal’s allocentric distance from his starting location along a route.

7. **Axis neurons: a novel form of spatial representation in the dorsal subiculum**

Jacob M. Olson and Douglas A. Nitz

Single neuron activity in the hippocampal formation discriminates individual locations and experiences. One utility of this stored information is as a source to create new spatial relationships that are generalizations of individual episodes. For example, the spatial concept of proximity to an edge exists in boundary vector cells of the subiculum. Their activity is likely related to the many place cells in CA1 that exist next to that edge. Only one synapse downstream from CA1 and with the most direct connectivity to known navigation structures in retrosplenial and parietal cortex, dorsal subiculum appears well positioned to begin the spatial generalization process. However, studies examining spatial firing properties of subicular neurons generally show quantitative and not qualitative distinctions between the two regions despite the very different connectivity. In this work, we recorded from dorsal subiculum while rats navigated on a complex navigation task. Enriching the behavioral and spatial structures creates a number of new spatial relationships, some of which are rather abstract or conceptual in nature. We found clear spatial correlates previously unreported in dorsal subiculum, likely a product of the enriched behavioral and spatial context. These include the presence of neurons having firing tuned to specific axes of travel. That is, these neurons exhibit peak activity in either of two head direction orientations that are 180-degrees apart. Such activity largely depended on the animal’s track running behavior, as it was far less apparent during open-field foraging. Nevertheless, such bi-directional (axis) tuning took the frame of reference of the larger environment as opposed to the track, a feature determined in experiments involving track rotation relative to the environment. Thus, the work identifies a new form of spatial representation in a brain region linking known navigation regions.
8. Schematic representations of local environmental space guide goal-directed navigation

Steven A. Marchette, Department of Psychology, University of Pennsylvania
Jack Ryan, Department of Neurology, University of Pennsylvania
Russell A. Epstein, Department of Psychology, University of Pennsylvania

To successfully navigate to a target, one must represent its location at multiple spatial scales. For example, to find a favorite coffee mug requires remembering that it is in one’s office and in the back corner. An intuitive hypothesis is that we accomplish this task by accessing the same representation at progressively finer levels of granularity—first remembering the general location and then “zooming in.” Here we provide evidence for a different view, in which independent representations are used for different spatial scales. Subjects in 7 experiments learned the location of objects positioned within four visually-distinct but geometrically-identical buildings that were situated within a broader virtual park. They were then tested on their knowledge of object location by asking them to navigate to the remembered location of each object. We examined errors during the test phase for confusions among geometrically analogous locations in different buildings—that is, navigating to the right location in the wrong building. We observed that subjects frequently made these confusions, which are analogous to remembering a passage’s location on the page of a book but not remembering the page that the passage is on. This suggests that subjects were recalling the object’s local location without recalling its global location. Further manipulations indicated that geometric confusions were observed even between buildings that were not metrically identical as long as geometrical equivalence could be defined. However, removing the walls so that the larger environment was no longer divided into subspaces abolished these errors entirely. Taken together, our results demonstrate that human spatial memory contains two separable representations of “where” an object can be found: (i) a schematic map of where an object lies with respect to local landmarks and boundaries; (ii) a representation of the identity of each local environment.

9. Spatial Instruction Generation for People with Varying Spatial Aptitudes

Gengen He - University of Nottingham Ningbo, Toru Ishikawa - University of Tokyo

This study aims to understand how people generate spatial instruction from their spatial experiences in the real world. A cognitive model has been generated based on an empirical built environment study of collaborative navigation behavior for people of varying spatial abilities in Tokyo, Japan. The participants are asked to navigate special routes in pairs simultaneously, then create spatial instructions simultaneously to another participant. Results from the study suggests that people of varying spatial abilities tend to use alternative methods for processing, organizing and selecting features in the environment to create spatial instructions. This spatial instruction model relates to other cognitive models that account for the difference in spatial processing. This model conceptually consists of “perception field”, “impression field”, “cognition field” and “spatial field” levels of processing. People of varying spatial abilities show varying results in picking up differing cues from the environment, gathering relevant information from what they see, selecting features from the environment, spatially constructing a mental map, then generating a cohesive spatial instruction to another person. Insights gained from this study has implications for better understanding individual differences in behavior and improving navigation system design, human computer interface, and spatial instructions for people of lower spatial abilities.


Mary O’Malley, Anthea Innes & Jan M. Wiener Bournemouth University, UK

Survey tasks that require a change in perspective - such as map reading - are particularly sensitive to the effects of cognitive ageing (Wilkiniss et al., 1997). This was also found in one of our recent studies (O’Malley et al, in preparation) in which we tested young and older adults’ memory of a recently learned route. Older adults, particularly those showing early signs of atypical ageing, showed specific deficits when asked to identify a schematic map of the route that they had just successfully learned, while they performed similar to age matched controls on other aspects of route knowledge. Although informative, a more ecologically valid scenario, that we address in this study, would be for participants to first study a “you-are-here” (YAH) map to plan and memorise a route before they execute it. In this experiment, young and older participants were repeatedly asked to study YAH maps in order to plan routes to goal locations marked on the maps. Once participants were confident that they had memorised the specific route plan, the map was taken away and they were asked to execute the route by navigating through the virtual care environment to where they thought the goal was. We found that older adults took longer to study and plan a route using the maps, and that they got to the goal location significantly less often than the younger controls. Additionally, older adults who showed early signs of atypical ageing performed worse than typically ageing adults. We will discuss the findings in relation to existing ageing research and the implications for navigational aids for older adults.
11. The Human Retrosplenial Cortex and Thalamus Code Head Direction in a Global Reference Frame

Jonathan P. Shine 1 José P. Valdés-Herrera 1 Mary Hegarty 2 Thomas Wolbers 1,3
1. German Center for Neurodegenerative Diseases (DZNE), Aging and Cognition Research Group, 39120 Magdeburg, Germany.
2. Department of Psychological and Brain Sciences, University of California, Santa Barbara, CA, 93106, USA.
3. Center for Behavioral Brain Sciences (CBBS), 39118 Magdeburg, Germany.

Spatial navigation is a multisensory process involving integration of visual and body-based cues. In rodents, head direction (HD) cells, which are most abundant in the thalamus, integrate these cues to code facing direction. Human fMRI studies examining HD coding in virtual environments (VE) have reported effects in retrosplenial complex and (pre-)subiculum, but not the thalamus. Furthermore, HD coding appeared insensitive to global landmarks. These tasks, however, provided only visual cues for orientation, and attending to global landmarks did not benefit task performance. In the present study, participants explored a VE comprising four separate locales, surrounded by four global landmarks. To provide body-based cues, participants wore a head-mounted display so that physical rotations changed facing direction in the VE. During subsequent MRI scanning, subjects saw stationary views of the environment and judged whether their orientation was the same as in the preceding trial. Parameter estimates extracted from retrosplenial cortex and the thalamus revealed significantly reduced BOLD responses when HD was repeated. Moreover, consistent with rodent findings, the signal did not continue to adapt over repetitions of the same HD. These results were supported by a whole-brain analysis showing additional repetition suppression in the precuneus. Together, our findings suggest that (i) consistent with the rodent literature, the human thalamus may integrate visual, and body-based, orientation cues, (ii) global reference frame cues can be used to integrate HD across separate individual locales, and (iii) immersive training procedures providing full body based cues may help to elucidate the neural mechanisms supporting spatial navigation.

12. Training recurrent neural networks to model how the brain might solve hard navigation tasks

Ingmar Kanitscheider Ila Fiete
Center for Learning and Memory and Department of Neuroscience University of Texas at Austin, TX, USA

Sensory noise and ambiguous cues make self-localization during navigation computationally challenging: Path integration causes location estimates to deteriorate quickly and landmarks are often spatially extended (e.g. walls) or look similar to other landmarks, thus providing only partial position information. Worse, in novel environments, landmark positions are unknown and must be learned while navigating. How brains perform these difficult computations is largely unknown. Engineering solutions require sophisticated probabilistic algorithms based on particle filters that update several hypotheses simultaneously over time, but are hard to map to biological neurons. We define several problems that crystallize typical navigation challenges: Self-localization in a circular 1D environment with several indistinguishable landmarks, known circular and polygon-shaped 2D environments with extended, featureless boundary walls, and novel 2D polygon-shaped environments whose boundaries have to be learned during navigation. We take a model-free approach and generate neurally plausible solutions by training recurrent networks with hidden layers, then scrutinize their performance, errors, and dynamics. The networks learn to update their estimates through velocity integration, integrate landmark information, and use memory of the last landmark encountered to choose between competing location hypotheses. The network performance matches the optimal particle filter (known environments) and substantially outperforms pure path integration (unknown environments), evidence that it can learn new maps. Reminiscent of remapping, the hidden units dynamically switch their tuning to code for the relevant statistics at a given time, such as location relative to the last observed landmark or to absolute location. These results demonstrate that hard navigation tasks can be solved by deterministic networks and provide predictions for neural representations during real-world navigational challenges.

Meredith Minear, Assistant Professor Department of Psychology University of Wyoming

A fundamental idea in research on behavior and motivation is that of approach and avoidance tendencies thought to be mediated by two different neural systems, a behavioral activation system (BAS) and a behavioral inhibition system (BIS) (Carver, 2006). Individual differences in behavioral activation and inhibition have been linked to individual differences in behavior, personality and decision making (e.g. Elliot & Thrash, 2002; Franken & Muris, 2005). We report data from three studies demonstrating a relationship between the behavioral activation/inhibition systems as measured by the BIS/BAS scales (Carver & White, 1994) and self-reported spatial anxiety (Lawton, 1994) and sense of direction (Hegarty et al., 2004) with individuals with higher BIS scores reporting greater anxiety in spatial navigation and worse sense of direction. Spatial anxiety was also negatively predicted by measures of BAS fun seeking and sensation seeking while sense of direction was not. These data support the hypothesis that individuals reporting greater behavioral inhibition feel less comfortable navigating an unfamiliar environment.

14. Effects of Aging on Landmark Recognition

Ramona Grzeschik(1), Ruth Conroy Dalton(2), Anthea Innes(3), and Jan Wiener(1)
1 Department of Psychology, Bournemouth University, Bournemouth, UK
2 Department of Architecture and Built Environment, Northumbria University, Newcastle, UK
3 Department of Applied Social Science, University of Stirling, Stirling, UK

Landmark recognition is essential for learning a novel route. However, not every object is a useful landmark, be it due to repetitive occurrence or visual appearance. Salient objects catching attention might be easier to memorize than non-salient objects, but if they appear more than once along the route, they can’t be used as a reliable landmarks. The aim of this study is to investigate how cognitive ageing affects people’s ability to select unique objects as landmarks. To do so, we created two kinds of routes through a virtual care home: simple routes and complex routes, each comprising four intersections each with two objects. For simple routes, the unique landmarks (objects that occurred only once along the route) were also salient. For the complex routes, in contrast, the salient objects occurred twice on the route (=non-salient) and the non-salient objects were unique. In this pilot study, we recorded route learning performance and gaze-behaviour from seven young and seven old (65+) participants. The gaze data revealed that older participants attended less to the unique landmarks on the complex routes than on simple routes, while younger participants primarily attended the unique landmarks, regardless their saliency. This effect was also reflected in the performance data: young participants did not show any performance difference in learning simple and complex routes, whereas the older participants performed better on the simple routes than on the complex routes. The preliminary results suggest that cognitive ageing affects the control of visual attention which, in turn, contributes to age-related deficits in route learning performance.

15. Defining Spatial Boundaries: A Developmental Study

Eugenia Gianni1, Laura De Zorzi1, & Sang Ah Lee1,2
1. University of Trento, 2. Columbia University

While navigation by boundary geometry has been widely documented, what defines a surface as a boundary have yet to be defined. Previous studies have shown that young children succeed in reorienting by 3D extended surfaces and that their size, salience, or stability do not influence their ability to use them. In contrast, children fail to use object arrays or high-contrast 2D forms to solve the task. What distinguishes a “boundary” surface from other environmental cues? What perceptual information determines whether something is represented as a boundary? How flexible is the concept of a boundary? We set out to answer these questions using a reorientation task with children from 2-7 years old. In Study 1, we minimized visual information while maintaining tactile and 3D structure using a rectangular arena consisting of transparent walls. We found that children begin to reorient successfully using the transparent surfaces around the fourth year of age. In contrast, children of all ages reoriented using opaque surfaces. In Study 2, we manipulated the continuity of the surface layout by testing children’s use of a rectangular configuration of 20 opaque freestanding objects (10 cm wide), arranged either with an inter-object spacing of 16 cm or 8 cm, and found that children only begin to succeed at around 7 years of age. These results suggest that boundary representations do not require visually opaque surfaces. By four years of age, children may flexibly incorporate transparent surfaces into their spatial mapping. In contrast, the ability to reorient using disconnected objects is acquired much later, even if the surfaces represent obstacles to vision and locomotion. This late ability to extrapolate a boundary from an array of objects may reveal a late-developing, more complex development of spatial abstraction and geometry. We discuss the results in light of potential underlying processes.

Dian Anggraini, Department of Psychology, Ludwig-Maximilians-Universitaet Muenchen; Graduate School of Systemic Neuroscience, Muenchen, Germany
Stefan Glasauer, Bernstein Centre for Computational Neuroscience, Muenchen, Germany
Klaus Wunderlich, Department of Psychology, Ludwig-Maximilians-Universitaet Muenchen

Studies on decision making reports that humans employ either a model-free repetition of successful behavior or a more demanding model-based approach to learn which decisions to make to maximize reward or avoid lost. A similar dual strategy approach, generally termed as route-based versus map-based strategy, exist when we navigate in novel environment. In this study, we aim to: 1) investigate the relationship of the neural process underlying of model-free vs. model-based decision making and route vs. map based navigation; 2) examine brain areas pertaining to computationally relevant signals during the spatial navigation. Twenty three healthy, right handed female between 21 to 29 years of age performed spatial decision task while undergoing functional magnetic resonance imaging (fMRI). The task consists of navigation within a 3D virtual reality 5 x 5 grid world. In the first session, subjects had to repeatedly find rewards located in fixed designated rooms promoting a route based strategy. In the further sessions, we encouraged map based planning of new routes by asking subjects to find particular rewards. We characterized subjects’ learning behavior by fitting several reinforcement learning (RL) type algorithm (model-free, model-based, and hybrid models) to explain subjects’ trial-by-trial choices. The reinforcement learning mathematical model provided a good fit to subjects’ behavior during spatial navigation. Thus, suggested that subjects’ choice behavior in a spatial decision task can be explained by an RL model. Importantly, we are able to distinguish between route based and map based navigation using weighted combination of model-free and model-based algorithm. Whole brain fMRI analysis shows that brain regions relevant for decision making - ventromedial prefrontal cortex (vmPFC), anterior cingulate cortex (ACC), orbitofrontal cortex - are also involved in the computations required during decision phase in spatial navigation.

17. *Representation of environmental shape in the hippocampal formation of domestic chicks*

Uwe Mayer1, Rachel Bhushan1, Giorgio Vallortigara1, Sang Ah Lee1,2
1. Center for Mind/Brain Science, University of Trento, Italy.
2. Department of Biomedical Engineering, Columbia University, USA.

The hippocampus plays an important role in spatial encoding and memory across various vertebrate species. In rodents, hippocampal neurons are particularly sensitive to a change in environmental geometry. Given the similarities in function between the mammalian and avian hippocampi, we aimed to measure whether a change in environmental geometry (square to rectangle) can differentially activate hippocampal cells in the domestic chick (Gallus gallus domesticus). During familiarization, we trained chicks to forage for mealworms in two square-shaped arenas connected by a door they had to walk through to get a reward. At test, one group of chicks (n=8) were exposed to a novel square arena (novel but identical to the training environment), another group (n=8) to a novel rectangle (same overall area), and a third group (n=7) to both the novel square and the rectangle. We processed the brains to visualize c-Fos immunoreactive neurons and found that chicks exposed to both a square and a rectangle exhibited a significantly higher neural activation than those exposed to just the square or just the rectangle (both of which were significantly higher in activation than a one-environment control group). This effect was particularly strong in the dorsomedial and dorsolateral regions of the hippocampus, which researchers have hypothesized to be homologous to the CA1 and entorhinal cortex of the rodent, respectively. For the first time in an avian species, we show that exposure to a transformation between two arenas of different geometric shape activates the hippocampus to a greater degree. We discuss these results in light of avian hippocampal function, considering the possible effects of environmental novelty and spatial mapping.
18. Boundary Coding in the Subiculum; Sensory Properties and Organization

Shailendra Rathore, Neil Burgess, Francesca Caccuci; University College London

The Hippocampal formation is focal in generating representations of space and supporting episodic memory. The recent discovery of boundary responsive cells in the Subiculum and Medial Entorhinal Cortex demonstrate the first explicit coding of environmental boundaries, with these cells responding to boundaries of the environment, inserted boundaries and traversable drops. The firing of these cells has been shown to be key to anchoring place and grid cells and may be a basis for place cell formation. How these neurons integrate sensory information about barriers is unknown and no model-driven approach has been developed to detect such responses.

We firstly show that most of the neurons in the Subiculum respond to an insertion of barrier, with many parametrically increasing their firing rate with barrier height. We confirm the existence of path integrative information in the Subiculum and show improvements in position decoding from Subicular ensembles in the presence of barrier. Secondly we demonstrate accurate classification of different boundary vector cell responses. Critically we show an unknown feature of boundary vector cells, that they possess a continuum of excitatory and inhibitory responses to barriers and these responses cluster together in terms of orientation in space - echoing centre-surround receptive field organization seen in visual cortex. These results advance our understanding on how sensory information about boundaries is encoded and organized in the activity of Subicular neurons.

19. Developing the Navigation Proficiency Assessment

Joshua W. Yudice 1, Dr. Virginia L. Flanagin 2
1 Center for Sensorimotor Research, Department of Neurology, Ludwig-Maximilians-University Munich, Germany
2 German Center for Vertigo and Balance Disorders, Department of Neurology, Ludwig-Maximilians-University Munich, Germany
2 Bernstein Center for Computational Neuroscience Munich, Ludwig-Maximilians-University Biocenter Planegg-Martinsried, Germany

Standardized assessments of navigation ability have been historically self-report inventories or assessments of correlated skills. In line with a recent movement to assess navigation ability directly using virtual environments, we are developing the Navigation Proficiency Assessment (NPA), which employs a series of randomly generated mazes that are navigated from the first-person perspective. We desired the NPA to be fast, unbiased, and to evaluate holistic navigation behavior in real-time. Unlike map retracing and distance and direction estimation, which assess a participant’s memory of the environment, the NPA is designed to assess behavior while it is being expressed. Progress through the mazes is tracked using proximity sensors in order to determine when a participant becomes lost. This intuitive measure of failure is used to pinpoint the threshold of maze difficulty that participants can reliably solve. We further sought to establish this method by evaluating the agreement of NPA scores with accepted self-report inventories. In a pilot experiment (N=26) we found a significant correlation with the Wayfinding Survey’s Response Score (r=-0.47,p=0.017). The Santa Barbara Sense of Direction Scale was administered in a second experiment (N=62) and a significant correlation was not found. The NPA is easy to administer and can be completed quickly, currently requiring 11.7 ± 5.2 minutes, which supports the NPA as a promising solution to the growing need for spatial ability assessment in medicine and education.

20. Visual landmarks sharpen grid cell metric and confer context specificity to neurons of the medial entorhinal cortex

José Antonio Pérez-Escobar, Laura Kohler, Olga Kornienko, Patrick Latuske, Kevin Allen Department of Clinical Neurobiology at the Medical Faculty of Heidelberg University and German Cancer Research Center (DKFZ) Heidelberg, Germany

The activity of neurons of the medial entorhinal cortex (MEC) is thought to generate a metric representation of space. We investigated how visual information impacts on this representation. Grid cell periodicity was strongly reduced when visual landmarks were eliminated. The loss of periodicity in darkness was associated with instability in the head-direction system. MEC speed cells changed their firing rate when visual landmarks were eliminated and the activity of border cells became less confined to the environment boundary. The firing rate of MEC neurons accurately predicted the presence of visual landmarks. Taken together, these findings demonstrate that visual information modulates the firing rate of spatially selective neurons within the MEC.
21. Grid cell firing rate encodes nonmetric contextual information
José Pérez-Escobar, Patrick Latuske, Olga Kornienko and Kevin Allen
Department of Clinical Neurobiology, Medical Faculty of Heidelberg University and German Cancer Research Center (Deutsches Krebsforschungszentrum), Heidelberg, Germany

Grid cells fire in regular intervals tiling the environment into a hexagonal pattern thereby providing a universal metric essential for measuring direction and distance travelled. As an animal moves, idiothetic cues from the vestibular and proprioceptive systems are integrated to continuously update the activity in the grid cell network. Environmental geometry, together with nonmetric context information, have been shown to control the positioning of the grid firing fields (Stensola et al., 2015, Krupic et al., 2015, Marozzi et al., 2015). However, it is not clear whether the firing rate of grid cells changes to reflect the presence of distinct nonmetric cues. We tested this hypothesis by recording the activity of grid cells while mice ran in a square open field and on a linear track. During the linear track recordings, two distinct LED arrays provided illumination and served as nonmetric contextual cues. Approximately a third of the grid cells changed their firing rate between the two contexts. Importantly, the spatial selectivity of the neurons was equivalent in the two conditions. These findings indicate that the rate-code of grid cells reflect nonmetric information, and suggest that contextual information is processed within the medial entorhinal network. Krupic, J., Bauza, M., Burton, S., Barry, C., and O’Keefe, J. (2015). Grid cell symmetry is shaped by environmental geometry. Nature 518, 232-235. Marozzi, E., Ginzberg, L.L., Alenda, A., and Jeffery, K.J. (2015). Purely Translational Realignment in Grid Cell Firing Patterns Following Nonmetric Context Change. Cereb. Cortex 25, 4619–4627. Stensola, T., Stensola, H., Moser, M.-B., and Moser, E.I. (2015). Shearing-induced asymmetry in entorhinal grid cells. Nature 518, 207-212. Acknowledgements This work was supported by an Emmy Noether Program grant (AL 1730/1-1) to KA and a Collaborative Research Centre (SFB-1134) from the DFG. The authors declare no competing financial interests.

22. Neuroanatomical analysis of the inputs into the retrosplenial head direction network
Han Yin Cheng, Pierre-Yves Jacob, Kate Jeffery

Head direction (HD) cells encode the directional heading of an animal’s head and are found in multiple brain regions, suggesting differences in the directional information encoded by each region. Extracellular recording in the retrosplenial cortex (RSC) has revealed a subpopulation of HD cells that anchor to local cues in preference to global cues. These local HD cells are found in the dysgranular RSC but not in the granular RSC. We are attempting to dissect the neural circuit underlying local and global cue anchoring by first looking at the projections to our implantation site in the dysgranular RSC using retrograde tracers. Van Groen and Wyss (1992) previously identified regions that project to the RSC and showed differential thalamic labelling along the rostral-caudal axis. We are attempting to replicate and extend their findings in order to discover the origin of the local vs global head direction activity. Initial retrograde tracing from our implantation site in the dysgranular RSC using fluorogold revealed substantial inputs from spatial processing regions including anterior thalamic nucleus, postsubiculum and claustrum, consistent with Van Groen and Wyss (1992). Quantitative analysis revealed substantial difference in the number of projection neurons labelled in the various anterior thalamic nuclei with substantially more labelling in the anteroventral and anteromedial nuclei as compared to the anterodorsal nucleus. Future dual retrograde tracing in dysgranular and granular RSC in the same animal will reveal qualitative and quantitative differences as well as similarity in the projections to the two distinct regions.

23. Boundary-related Neural Activity in the Human Hippocampal Formation
Sang Ah Lee1,2, Jonathan Miller2, Tom Coffey3, Michael Sperling4, Ashwini Sharan4, Ali Asadi-Pooya4, Gregory Worrell5, Brent Berry5, Barbara Jobst6, Kathryn Davis7, Timothy Lucas7, Sameer Sheth8, Catherine Schevon8, Michael Kahana9, Sandy Das9, Joel Stein7, Daniel Rizzuto9, Joshua Jacobs2

iNAV 26 - 30 june 2016 18 Errors and omissions excepted.
Environmental boundaries play a major role in spatial representation across a wide range of tasks, from early navigation abilities in children, to place learning in virtual reality environments, to 2D visual scene recognition. The neural correlates of boundary representations (i.e., boundary/border cells) have thus far been most widely studied in the rodent hippocampal formation. Nevertheless, converging evidence from a wide range of species and methodologies suggests that the neural correlates of spatial navigation are widely shared across vertebrates. Therefore, while the human correlate of boundary cells have not yet been discovered, it may be possible to detect boundary-specific neural activity in the human brain, particularly in the entorhinal cortex and subiculum where boundary-related neurons exist in rodents. In this study we tested neurosurgical patients implanted with intracranial electrodes in a virtual navigation task with varied goal locations across trials. Here we present comparisons of neural oscillations on trials in which subjects encoded goal locations near environmental boundaries to trials in which they encoded goal locations in the central region of the arena. In general, we find higher theta power for goals near the boundaries of the arena. We further investigate these effects in specific hippocampal subregions of interest and discuss their implications for boundary coding in the human brain.

24. Human Spatial Accuracy in an Open Field Virtual Environment

Christopher Roppelt [1,2], Virginia F. Flanagan [1]
[1] German Center for Vertigo and Balance Disorders (DSGZ)
[2] Graduate School of Systemic Neurosciences (GSN-LMU)
Ludwig-Maximilians-Universität Munich, Germany

Virtual environments (VEs) are a common means to investigate spatial cognition in humans and animals. So-called open field VEs, derived from real open field environments used to study neuronal activity in rodents, have become particularly important in the study of human place-encoding neurons such as place cells and grid cells. Typical paradigms test participants' location memory at different places across the VE, while simultaneously recording their brain activity. Participants' positions in the VE are then correlated with the measured brain activity to infer its place-encoding characteristics across the VE's space. This association assumes a constant spatial precision across the VE, participants' behavior is not likely to be consistent across space. A systematic description of human spatial accuracy in different locations of an open field VE is still lacking. To test this, we employed a location recognition task in a quadratic VE enclosed by four differently colored walls. 36 target locations were arranged at the intersections of an equidistant 6x6 grid covering the space within the walls. Participants were placed inside the VE and asked to collect an object randomly appearing at one of the target locations. After reorientation, they had to return the object to its original (i.e., target) location. The distance between the returned and the target position, the distance error, was analyzed. We found an increase in the distance error's magnitude from the VE's borders towards its center, with the error direction changing systematically depending on the two closest walls at each target location. This suggests that participants' internal representation of an open field VE is not uniform across its space, and that precision of participants' spatial perception depends on the distance from salient cues. A behaviorally appropriate association between neural activity and spatial location can bring us new insights into the functional relevance of these neurons.

25. Place cell assembly dynamics during exploration in darkness

Olga Kornienko, José Antonio Pérez-Escobar, Patrick Latuske and Kevin Allen
Department of Clinical Neurobiology at the Medical Faculty of Heidelberg University and German Cancer Research Center (DKFZ), Heidelberg, Germany

The hippocampus plays a fundamental role in spatial behavior integrating external cues as well as internal information from the vestibular and proprioceptive systems. Hippocampal place cell assemblies provide an internal representation of the animal's location, but how is this representation modified when visual landmarks are eliminated? We examined the activity of CA1 neurons in mice running on an elevated circular platform, alternating between 2-min light and dark trials. The location of the polarizing light source during light trials was varied across trials. Our findings show that in light trials the rotation of visual landmarks caused an equivalent reorientation of place fields, while pairwise correlations of instantaneous firing rates (IFR) between cells were preserved. In contrast, when the light was turned off approximately 80% of the cells changed their firing activity significantly and there was a significant change of IFR pairwise correlations. Additionally, removing visual cues caused a rapid decrease in stability of spatial firing patterns and a reduction in spatial information. We examined neuronal population dynamics during light and dark conditions, detecting cell assemblies by independent component analysis. Assemblies exhibited stable spatial activity in light but not in dark trials. More importantly, different conditions triggered the activation of distinct assemblies. Current results suggest that removal of visual landmarks causes a global activity change from one internal representation to another. Acknowledgements This work was supported by an Emmy Noether Program grant (AL 1730/1-1) to KA and a Collaborative Research Centre (SFB-1134) from the DFG.
26. *In vivo characterization of Calbindin and Reelin expressing neurons in the medial entorhinal cortex*

Oana Toader, Antonio Caputi, Kevin Allen and Hannah Monyer
Department of Clinical Neurobiology at the Medical Faculty of Heidelberg University and German Cancer Research Center (DKFZ), Heidelberg, Germany

The superficial layers of the medial entorhinal cortex (MEC) are composed of several anatomically distinct excitatory neurons. It was recently proposed, based on anatomical and in vitro electrophysiological properties, that excitatory neurons can be classified into four cell types: pyramidal, intermediate pyramidal, stellate and intermediate stellate cells. Their firing properties in intact animals are still largely unknown. Two mutually exclusive molecular markers are expressed differentially in these cell types, with the pyramidal and intermediate pyramidal expressing Calbindin (CB) and the stellate and intermediate stellate expressing Reelin (RE). To investigate the firing properties of the different cell types in behaving animals, we used two Cre mouse lines to selectively express ChR2 in CB+ and RE+ cells (CB-Cre and Uchl1-Cre, respectively). Mice were implanted with 4-5 tetrodes and an optical fibre in the medial entorhinal cortex and were trained to run in a square open field. We recorded 1022 and 580 neurons in CB-Cre and Uchl1-Cre mice, respectively. We focused our analysis on neurons that had either a light-activation latency lower than 2 ms or a jitter (first spike latency SD) lower than 0.65 ms (n=47 CB+ and n=43 RE+). Preliminary analysis of all selected neurons revealed no significant difference in the average firing rate, spatial information score, theta vector length or speed modulation. The RE+ group contained a slightly higher percentage of grid cells (27% compared to 17%, p=0.21, Chi square test). Further analysis will show whether the functional connectivity between excitatory and fast-spiking interneurons differs between the two cell populations.

27. *Impaired landmark anchoring of postsubiccular head direction cells in rats with bilateral lesions of the lateral geniculate nucleus*

James Street, Pierre-Yves Jacob, Yave Navarro, Kate Jeffery
Institute of Behavioural Neuroscience, 26 Bedford Way, University College London, WC1H 0AP

Navigation using allocentric frames of reference necessitates the use of external landmarks to orient accurately in an environment. At the single-unit level, head direction (HD) cells, found in multiple areas of the rat brain, encode the directional bearing of a rat by displaying a greater firing rate when the animal faces the cell’s preferred firing direction. HD cells ‘anchor’ their firing to available distal visual cues, such that the tuning curve of the cell will shift to follow rotational transformations of these cues. Two visual processing pathways exist in mammals. The geniculo-cortical pathway likely inputs visual information to the postsubiculum via projections from the primary visual cortex. Within the subcortical pathway, the pulvinar forms a major component of the dorsal visual stream (Kaas & Lyon 2007), classically involved in visual attention and “where” information processing, and projects via posterior parietal cortex to the retrosplenial cortex. Subcortical vision is less well-studied in rodents than primates, and the extent to which it may guide action, including in navigation, remains debated. In particular, it is unknown whether this pathway may support landmark anchoring of spatially modulated cells in the absence of intact visual cortical inputs. Here, we present HD cells recorded extracelularly from the postsubiculum of freely roaming rats with bilateral lesions of the lateral geniculate nucleus, silencing inputs from the cortical pathway into the HD system. Rats foraged in a cylinder containing two high-contrast visual cue cards at 180 degrees that were rotated together by a random angle between trials. Recorded HD cells did not consistently rotate their tuning curve to follow cue manipulations, but instead shifted randomly or did not shift between trials, indicating that cortical vision is required for visual anchoring of these cells and suggesting a minimal role for the subcortical pathway in the processing of salient visual landmarks.

28. *The metric properties of the grid cell map are modified in a 1D space*

Fabrizio Capitano1, Pierre-Yves Jacob1, Bruno Poucet 1, Etienne Save1, Francesca Sargolini1
1-LNC (UMR7291), Fed 3C, AMU-CNRS, Marseille (France)

The function of grid cells in spatial cognition is not fully understood. Previous studies have suggested that grid cells provide an invariant self-movement-based map of the environment. However, this hypothesis has been challenged by recent studies demonstrating that modifications of the environment affect grid cell activity. Here we show that in a familiar 1D continuous environment (a circular track) grid cells display a novel 1D regular map whose firing fields tend to be more spaced than in the 2D hexagonal grid map. Moreover, in the 1D track but not in the 2D arena, field spacing is dependent on the size of the environment. Our results indicate that the grid map metric properties are shaped by the external environment.
29. **Object representation along the proximo-distal axis of CA1**

Brianna Vandrey*, James A. Ainge* (*University of St Andrews)

Models of medial temporal lobe function often suggest that the spatial and non-spatial content of episodic memory reaches the hippocampus via the medial entorhinal cortex (MEC) and lateral entorhinal cortex (LEC), respectively. However, recent evidence suggests that the LEC plays a critical role in binding these two types of information together prior to the hippocampus. The LEC contains neurons which are spatially tuned to objects in the environment, and damage to this structure impairs performance on object-based associative memory tasks. Notably, object-related firing in the LEC strongly resembles object-modulation of place cells in the hippocampus; neurons in both structures encode object location, respond to object displacement, and fire at locations where an object was previously located. Therefore, it is possible that LEC input drives the spatial representation of objects in the hippocampus. We investigated this by implanting microdrives in rats (n=5), with tetrodes targeting either the proximal or distal CA1. These regions receive differential input from the EC, so this strategy permitted us to record from populations of neurons which primarily receive MEC or LEC input.

Place cells were recorded during exploration in an open-field containing objects which underwent spatial manipulations, including object dislocation and novel object-place recognition. Object-modulated and non-object-modulated cells were recorded in both regions. Preliminary analysis suggests that LEC input results in greater influence of objects on place cell firing. Given that objects might shape representations of an environment by functioning as landmarks, these findings influence our understanding of how entorhinal-hippocampal communication supports spatial memory and navigation.

30. **Individual differences in spatial ability**

Virginia L. Flanagan1, Kerstin Wenzel2, Eva Fraedrich1, Lilianne R. Mujica-Parodi3, Stefan Gläsauer1
1 Dept. of Neurology and German Center for Vertigo and Balance Disorders, Klinikum der Universität Munich
2 Neurocognitive Psychology, LMU Munich
3 Department of Biomedical Engineering, Stony Brook University, New York

The successful encoding and subsequent navigation through an environment is a complex process involving perceptual and memory functions as well as the ability to manipulate and update information across time and space. Humans differ greatly in their ability to successfully navigate their surroundings. These individual differences in spatial navigation may be related to a propensity toward one spatial ability over another. If so it would be important to know what spatial abilities covary and what components of spatial navigation are affected. To examine this, a group of healthy participants (N = 25) were tested on the following: 1) visuospatial memory in a cued associated place-picture recall task, 2) visual attention in a “spot the difference” task, 3) a three-dimensional mental rotation task, 4) a vestibular-proprioceptive self-rotation perception task and 5) the Santa Barbara Sense of Direction Scale. To test spatial navigation ability participants were asked to navigate through a set of virtual mazes with only one solution. The maze task had an exploration phase in which participants learned the virtual environment, a forward phase where participants traveled as fast as possible from the start to the end of the maze, and a return phase in which participants were asked to go back the same path they came, as quickly and as accurately as possible. Participants differed greatly in their ability to perform the maze task; the return phase was particularly difficult for some participants. A better return time was correlated with a higher score on the mental rotation task. Performance in the “spot the difference” task correlated positively with performance in the spatial memory task. These results allow us to characterize how component spatial skills contribute to overall navigation behavior, and may help us explain individual differences in spatial navigation.

31. **Human hippocampal theta modulations as a function of virtual movement speed and memory performance**

Jonathan Miller and Joshua Jacobs, Columbia University

Electrocorticoegraphic (ECoG) recordings from human hippocampus have shown increases in low frequency power associated with periods of virtual movement compared to periods of stillness, yet these previous tasks were not designed to explicitly examine the effects of movement speed. We designed a virtual spatial navigation and memory task well suited to elicit low frequency activity while systematically modulating speed of movement. Using data from neurosurgical patients with hippocampal depth electrodes, we provide evidence that movement related theta oscillations in human hippocampus reliably appear at lower (between 1-4 Hz) frequencies than in rodents and increase in power as movement speed increases. In addition, we use multivariate statistics to untangle the relative contributions of movement speed, memory performance, and voluntary vs involuntary movement to the overall spectral signal.
32. **Simultaneous encoding of local and global head-direction reference frames by dysgranular retrosplenial neurons**

Pierre-Yves Jacob 1, Giulio Casali 1, Dorothy Overington 1, Laure Spieser 2 & Kate J Jeffery 1 1 - University College of London, Institute of Behavioural Neuroscience, Department of Experimental Psychology, Division of Psychology and Language Sciences, London
2 - City University of London, Department of Psychology, London

Head direction (HD) cells are neurons that fire when the animal’s head faces in a particular direction in space, and provide the sense of direction for spatial orientation and navigation. These neurons, found in multiple brain regions, express a global directional signal that is highly coherent. The retrosplenial cortex (RSC) contains HD cells, and is hypothesized to play a primary role in processing stable visual landmarks. The RSC has also been shown to encode different connected local spaces rather than a global reference frame. In this study, we questioned whether and how the RSC HD cells encode visually defined local reference frames. We recorded HD cells while rats freely moved in two visually symmetrical compartments polarized by a cue card and connected by a central door. In order to resolve the visual ambiguity, each local compartment was scented by a specific odour. We report that HD cells could use olfactory cues to break the symmetry of the rotationally symmetric two-compartment environment, and thus express a coherent encoding of the global reference frame. Interestingly, we found simultaneously a sub-population of neurons (n=116) which fired in a given direction in one compartment and rotated (“flipped”) their directional activity by 180° in the other compartment, independently of the main HD signal. These flipping HD cells were recorded in the dysgranular RSC, and not in the granular RSC nor in two other HD regions, the postsubiculum and the anterodorsal thalamic nucleus. Furthermore, a third neuronal population exhibited bimodal HD activity even within a local compartment, suggesting a possible learned interaction with the main HD cell signal. The finding that RSC HD neurons can operate independently of the main HD signal overturns the previous assumption of a global, unitary head direction signal; that this is controlled by environmental cues suggests a specific role for dysgranular RSC in landmark-based directional encoding of local sub-spaces.

33. **Navigation in a complex environment: learning effects of use-dependent local sleep in wake and daytime nap.**

Quercia A.(1), Zappasodi F.(1,2), Commiteri G.(1,2), Pizzella V.(1,2), Ferrara M(3).
1 Department of Neuroscience, Imaging and Clinical Sciences, “G. d’Annunzio” University of Chieti-Pescara, Italy
2 Institute for Advanced Biomedical Technologies “ G. d’Annunzio ” University of Chieti-Pescara Chieti - ITAB, Italy
3 Department of Life, Health and Environmental Sciences, University of L’Aquilia, Italy

Spatial memories benefit from sleep. Slow Wave Activity (SWA), the hallmark of sleep plasticity, increases locally in the brain regions engaged by a previous learning task. Recent evidence showed error-related local and use-dependent sleep also during wake in task-related neuronal groups. The present study investigates the functional role of local sleep during an intensive spatial navigation task and after a daytime nap. The spatial navigation task (SN) was based on the Cognitive Map Test (CMT) by Iaria and colleagues. Participants (n=33 males) were required to form a mental representation of a virtual city and to use it to travel between 16 different Landmarks (retrievals, continuously repeated for about 1.5 h). Then, the Nap group (n=13) was allowed to sleep, the Quiet wake group (n=10) laid down with eyes closed, the Active wake group (n=10) performed an audiobook listening task. Re-tests (new retrievals) were performed at the end of each protocol. In a separate session, the Nap group performed a Control Task (CT: defined route navigation without learning) and a subsequent nap. All the sessions were recorded with video high-density electroencephalogram (hd-EEG, 128 channels). After performance stabilization (trend analysis), subjects progressively made errors on well-learned retrievals, which positively correlated with the best hits obtained before the stabilization. Nonparametric statistical test for multiple comparisons (p<0.05) showed that delta power (1-4 Hz) increased locally and progressively during SN, both referred to errors and with respect to CT. Instead, theta power (4.5-7.5 Hz) did not differentiate between the tasks. Local increase of SWA was selectively observed during the post-SN nap. Finally, only the Nap group showed a significant improvement of spatial performance at retest. In conclusion, local sleep in wake and after a nap appears to be functionally relevant for complex environmental learning through spatial navigation.
34. *Prioritization of hippocampal- versus striatal-dependent spatial memory across the human lifespan*

Franka Thurm1, Nicolas W. Schuck2, Shu-Chen Li1
1 Lifespan Developmental Neuroscience, Department of Psychology, TU Dresden, 01062 Dresden, Germany
2 Princeton Neuroscience Institute, Princeton University, USA

Both the hippocampus and the striatum play important roles in spatial learning and memory. Whereas complex representations of spatial layouts, including boundary-location relations, are supported by the hippocampal formation, computationally less demanding cue-based navigation strategies are mainly subserved by the striatum. Previous work of our group indicated that both normal aging and dopamine (DA) dysfunction in Parkinson’s disease (PD) affect the prioritization of navigation strategies. In contrast to young adults, healthy older adults and PD patients prioritized striatal cue-based over hippocampal boundary-related navigation strategies. Furthermore, DA medication in PD patients had differential beneficial effects on striatal- versus hippocampal-dependent spatial memory. We investigated the development of cue-based versus boundary-dependent spatial memory in younger (6-8 years) and older children (10-13 years), adolescents (15-17 years), young adults (20-35 years), and healthy older adults (65-80 years) using a virtual reality task. Our results show that whereas striatal-dependent cue-location memory seems to develop early (i.e., after the age of 8 years) and is less affected by aging-related decline, hippocampal-dependent spatial memory of boundary-location relations follows an inverted U-function with deficits being largest in young children and older adults. Furthermore, trial-by-trial reaction time variability during a perceptual speed task was positively correlated with a shift towards greater reliance on cue-based navigation strategies. The development of boundary-dependent spatial navigation is consistent with previous animal research on hippocampal spatial function and resembles the inverted-U function relating DA signaling to cognitive performance across the lifespan. Taken together, our study provides a lifespan perspective pointing to differential development and aging of spatial learning and memory subserved by the hippocampal-striatal circuitries.

35. *Phase synchronization in the human medial temporal lobe predicts the precision of spatial memory encoding: Evidence from intracranial recordings*

Andrew J. Watrous1, Brad Lega9, Michael Sperling3, Ashwini Sharan4, Gregory Worrell5, Barbara Jobst6, Robert Gross8, Joel Stein10, Sandhitsu Das11, Daniel Rizzuto2, Michael Kahana2, Joshua Jacobs1
1 Department of Biomedical Engineering, Columbia University 2 Department of Psychology, University of Pennsylvania 3 Department of Neurology, Thomas Jefferson University Hospital 4 Department of Neurological Surgery, Thomas Jefferson University Hospital 5 Department of Neurology, Mayo Clinic 6 Department of Neurology, Dartmouth University 8 Department of Neurosurgery, Emory University 9 Department of Neurosurgery, University of Texas-Southwestern 10 Department of Radiology, Hospital of the University of Pennsylvania 11 Department of Computer and Information Science, University of Pennsylvania

Lesion and fMRI studies have identified the hippocampus and adjacent cortical areas in the medial temporal lobe (MTL) as critical areas for spatial memory encoding, although the electrophysiological basis for spatial encoding is less clear. Prior invasive MTL studies have implicated oscillatory phase as a possible mechanism for coordinating activity within and between different MTL structures during episodic encoding. Here, we asked whether similar phase based mechanisms support spatial encoding by testing patients with pharmaco-resistant epilepsy on a virtual Morris water maze task. Patients were able to successfully encode an object location in the environment and return to this location during a retrieval test. Assessing phase synchronization between all MTL electrodes in more than 40 patients in the low and high theta bands, we found that particular phase relations between MTL subregions was related to the precision of spatial encoding. These observations 1) were statistically robust both on individual electrode pairs and in the majority of patients, 2) were strongest in the slow theta/delta band, and 3) showed subregionally specific effects in right MTL regions, particularly CA1. These findings further implicate slow theta phase as a mechanism of information representation and transmission in the human MTL.
36. **Goal representation in the hippocampus**

Eléonore DUVELLE [1,2,3], Vincent HOK [1], Bruno POUCET [1], Angelo ARLEO [2], Etienne SAVE[1]


The hippocampus is thought to play a crucial role in spatial navigation. Hippocampal pyramidal cells, or ‘place cells’, provide a representation of one’s location in a given environment. In tasks such as random foraging place cells generally express one ‘place field’, a spatially localized area of high activity. In more cognitively demanding tasks, the spatial hippocampal signal appears to incorporate extra-spatial activity. In particular, in a task where rats had to reach an unmarked location to get a reward, a large majority of place cells showed a secondary activity while the rat was waiting at the goal. This secondary activity was hypothesised to be relevant for goal representation, but its precise nature – whether spatial or reward-related – is still unknown.

We designed a task where rats could freely choose between two unmarked goal locations of varying value – each goal could provide 3, 1 or no food pellet. Rats trained in this task accurately assessed the current goal value, adapting their choices according to experimental conditions. Extracellular, single-unit recordings from CA1 and CA3 hippocampal regions showed goal-related activity at the two goal locations. Our results suggest that the hippocampal goal-related signal is mainly of spatial nature, discriminating between the two goals at the population level. Interestingly, this signal was independent from goal value. Last but not least, we observed that active place cells were not the only ones to contribute to the goal-related signal: ‘silent cells’, usually merely detectable, also contributed to this goal-related activity. Overall, our findings suggest that when an animal is performing a spatially demanding task, its hippocampus is engaged to store relevant information about the spatial characteristics of the goal. Used in cooperation with structures involved in decision-making, this hippocampal goal representation could support fine optimisation of goal-directed navigation.

37. **To Teach A Mockingbot: Dopamine-Modulated Songbird Learning in Robot Navigation and Control**

Jake Bruce and Michael Milford - Queensland University of Technology

Songbirds produce long and complex vocalization sequences that are highly similar within social groups. A songbird memorizes tutor songs heard during early development, and learns to reproduce these memorized sequences through motor exploration. Some songbirds, such as the brown thrasher, can learn and recall more than a thousand distinct songs. We present a computational model capturing the processes of memorization, motor exploration, comparison to tutor sequences, and reinforcement that can explain aspects of this learning process. In particular, the model suggests a mechanism for how thousands of sequences that share common elements can be stored in the same neural substrate without collision or catastrophic forgetting. The model is based on the architecture of the songbird basal ganglia loop, homologs of which are thought to exist in mammals and insects as well. Although the bird song system is typically investigated in the context of vocal learning, it may suggest how learning could be accomplished in other diverse domains such as manipulation, flight control, and navigation. We are using robots to investigate the ability of the model to learn many overlapping sequences in multiple domains, including learning hundreds of distinct paths through complex environments. We expect embodied robot experiments to elucidate problems (such as those related to imperfect sensing and actuation) that are difficult to address in simulation experiments due to the intractability of simulating the real world with high fidelity. The complexity with which animals are forced to cope is likely to be important for truly understanding the behaviour of neural systems, and robotic experiments ensure the problems involved are realistic and unavoidable.
38. Sex differences in behaviour and EEG during the performance of two navigation tasks

Erin L Zelinski, Mashal Fida, Robert J Sutherland
Canadian Centre for Behavioural Neuroscience, Department of Neuroscience, University of Lethbridge, Alberta Canada

Research on the neurobiology of spatial abilities often requires human subjects to be stationary. Consequently, virtual reality is a commonly used tool for elucidating how we process information about the world around us. However unlikely, the absence of movement may change the nature of the spatial representation. Thus, we developed a real world, dry version of the Morris water task to assess whether human subjects would perform similarly to other animals and human performance on virtual spatial tasks. We hypothesized the strategy implemented by subjects would differ by sex and that performance accuracy would reflect the strategy used. Results indicate that males and females implement allocentric and egocentric strategies respectively and that males tended to be more accurate unless they were required to use an egocentric strategy. Subjects also appeared to orient themselves using different cue types. A virtual task was developed to examine the types of cues each sex uses when solving an object-location task. During exploration, subjects moved through the environment until they encountered all object-location pairs. During phase two, subjects were shown pictures of objects with backgrounds that were either congruent with the original object-location pair, incongruent, or novel. Scalp EEG was recorded during task performance and responses to the presentation of congruent, incongruent, and foil scenes were compared in the time-frequency domain. The final phase of the task required subjects to place objects in their encountered positions over a topographical representation of the environment. Sex differences in accuracy and the types of information used to solve the task were observed. We propose that sex differences are not the result of superior abilities in males, rather allocentric strategies incorporate more precise spatial information whereas egocentric strategies contain more information about environmental features.

39. Environment size affects stability of head direction cell firing in pre-eye-opening rat pups

JP Bassett, F Cacucci, TJ Wills
University College London

Head direction (HD) cells have previously been recorded in the anterodorsal thalamic nucleus (ADn) and dorsal presubiculum of pre-weanling rat pups as early as postnatal day 12. Before eye opening, HD cell firing is characterised by low spatial information content and directionally unstable firing, both within and between trials. In the ADn, HD cell number, information content, and stability increase with age, with the greatest increases coinciding with eye-opening. In the present study, we recorded HD cells in the ADn of rat pups before eye-opening, in two square environments alternately: one 62 cm per side as in our previous study, and a second with approximately 1/3 the area of the first (35 cm per side). We found that HD cells that were unstable in the large environment were stabilized by the small environment, including cells so unstable in the large environment as to fail the classification threshold as HD cells. When groups of these simultaneously recorded unstable cells were analysed over short time periods, the order of firing bursts between cells was predicted by the direction of head turn, and the angles separating them remained approximately consistent, indicating that the structure of the directional network was in place even when the directional firing was very unstable. We conclude that before eye-opening, the HD cell network is not only in place, but can represent allothetic direction in a stable and nearly adult-like manner, if the nature of the local environment allows it. Previous descriptions of HD cells recorded in rat pups before eye-opening have therefore likely underestimated their number, peak firing rate, and potential to carry directional information as a result of recording in large environments. We speculate that the reasons for stable HD signalling in the small environment may include increased contact with local boundaries and changed path features, which may reduce path integration error in the absence of visual input.

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Errors and omissions excepted.
40. A novel navigation task for studying planning in the rodent brain

Michael Pereira(1), Christian K. Machens(1), Rui M. Costa(1), Thomas Akam(1).
(1)Champalimaud Neuroscience Programme, Champalimaud Centre for the Unknown, Avenida Brasilia, Docas de Pedrouços, Lisboa 1400-038, Portugal

Planning consists of the use of a cognitive map linking states through actions, allowing behavioral trajectories to be simulated. Planning mechanisms are thought to coexist in the brain with other decision making strategies, including those based on trial-and-error learning and heuristics. Though many decision problems can only be solved optimally through planning, action recommendations generated by different strategies often coincide, making it hard to disambiguate them.

We developed a novel navigation task which quantitatively isolates the contribution of planning to rodent navigation. Mice navigate a tortuous elevated maze to collect reward. On each trial, 1 out of 36 possible goal locations is cued with a stimulus light, the mouse navigates to the cued goal to receive a reward. Another randomly selected goal location is then cued to start the next trial.

The non-repeating sequences of reward locations minimize the utility of habitual strategies, while the tortuous maze structure causes planning and directional heuristic to give different recommendations, and rewards planning with shorter routes to goal. The modular design of the apparatus yields a large space of possible maze configurations, from which those which optimally dissociate planning from heuristic strategies can be chosen.

Mice perform hundreds of trials in a single session and that their trajectories decrease in length with training. Analysis of choice behavior at decision points reveals mice tend to more often choose actions preferred by planning than actions preferred by a directional heuristic. A mixture of strategies model fit to the data also indicates a significant component of planning. Both measures of planning are found to increase over the course of training. We anticipate the task will be a powerful tool for studying the neural circuit basis of route planning.

41. Absence of visual input results in the disruption of grid cell firing in the mouse

Guifen Chen, University College London

Grid cells are spatially modulated neurons within the medial entorhinal cortex, whose firing fields are arranged at the vertices of tessellating equilateral triangles. The exquisite periodicity of their firing has led to the suggestion that they represent a path integration signal, tracking the organism’s position by integrating speed and direction of movement. External sensory inputs are required to reset any errors that the path integrator would inevitably accumulate. Here we probe the nature of the external sensory inputs required to sustain grid firing, by recording grid cells as mice explore familiar environments in complete darkness. The absence of visual cues results in a significant disruption of grid cell firing patterns, even when the quality of the directional information provided by head direction cells is largely preserved. Darkness alters the expression of velocity signalling within the entorhinal cortex, with changes evident in grid cell firing rate and the local field potential theta frequency. Short-term (<1.5s) spike timing relationships between grid cell pairs are preserved in the dark, indicating that network patterns of excitatory and inhibitory coupling between grid cells exists independently of visual input and of spatially periodic firing. However, we find no evidence of preserved hexagonal symmetry in the spatial firing of single grid cells at comparable short timescales. Taken together, these results demonstrate that visual input is required to sustain grid cell periodicity and stability in mice, and suggest that grid cells in mice cannot perform accurate path integration in the absence of reliable visual cues.
42. Functional specialization of the posterior cingulate in spatial updating and orienting

Ford Burles, Edward Slone, Giuseppe Iaria. NeuroLab, Department of Psychology, Hotchkiss Brain Institute, and Alberta Children's Hospital Research Institute, University of Calgary, Calgary, Alberta, Canada, T2N 1N4.

The retrosplenial complex is a region within the posterior cingulate cortex implicated in spatial navigation. Here, we investigated the functional specialization of this large and anatomically heterogeneous region by using fMRI and resting-state functional connectivity combined with a spatial task with distinct phases of spatial ‘updating’ (i.e. integrating and maintaining object locations in memory during spatial displacement) and ‘orienting’ (i.e. recalling unseen locations from current position in space). Both spatial ‘updating’ and ‘orienting’ produced bilateral activity in the retrosplenial complex, among other areas. However, spatial ‘updating’ produced slightly greater activity in ventro-lateral portions, of the retrosplenial complex, whereas spatial ‘orienting’ produced greater activity in a more dorsal and medial portion of it (both regions localized along the parieto-occipital fissure). At rest, both ventro-lateral and dorso-medial subregions of the retrosplenial complex were functionally connected to the hippocampus and parahippocampus, regions both involved in spatial orientation and navigation. However, the ventro-lateral subregion of the retrosplenial complex displayed more positive functional connectivity with ventral occipital and temporal object recognition regions, whereas the dorso-medial subregion activity was more correlated to dorsal and frontal activity, as well as negatively correlated with more ventral parietal structures. These findings provide evidence for a dorso-medial to ventro-lateral functional specialization within the human retrosplenial complex that may shed more light on the complex neural mechanisms underlying spatial orientation and navigation in humans.